QUALITATIVE AND QUANTITATIVE ANALYSES OF THE SONG OF THE EAST AUSTRALIAN POPULATION OF HUMPBACK WHALES

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Humpback whales produce a complex sequence of vocalisations, called songs, while on migration paths and breeding grounds. While its function remains unclear, the association between song and its production during the breeding season has lead to the hypothesis that song may be an acoustic display used by males to attract potential mates and repel rival males. If so, significant differences in the song between singers might be expected. Here we describe the structure of the song off east Australia in 1998 and present a quantitative comparison of the acoustical characteristics of two sound types between six individual singers to determine the extent that these provided discrimination between individuals. The song was found to consist of five themes produced in a fixed order, consistent with other observations of humpback whale song. Multivariate and univariate tests showed significant measurable differences between individuals for all acoustical parameters included in the analysis. However, for any parameter, the differences were accounted for by one or two individuals and there was no observable pattern or consistent differences between individuals. Canonical analysis showed substantial overlap between clusters suggesting poor discrimination between individuals. The frequency of different units of the same sound type varied by less than two semi-tones for an individual and no more than three semi-tones between individuals, suggesting that humpback whales have a well refined perception of pitch. We conclude that while there were differences between individuals in the characteristics of the two sounds analysed, these did not provide useful discrimination between individuals. ❒ *Humpback whale, song structure, Australia.*

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Humpback whales, *Megaptera novaeangliae*, migrate annually from high latitude feeding grounds in summer to low latitude tropical waters to breed and calve during winter (Chittleborough, 1965). During this migration humpback whales produce a complex sequence of vocalisations known as 'song' (Payne & McVay, 1971).

The function of song remains unclear. There is evidence that only male humpback whales sing (Glockner, 1983; Baker & Herman, 1984) and singing appears to be confined to the migration pathway and breeding grounds. This relationship with the breeding season has given rise to the hypothesis that song is a powerful acoustic display for attracting mates (Tyack, 1981; Winn & Winn, 1978; Frankel, 1994). However, other explanations include a spacing function among males (Frankel et al., 1994) and a means of establishing a dominance hierarchy (Darling et al., 1983). Multiple use of acoustic displays such as song is not uncommon and is well documented in many bird species (Catchpole & Slater, 1995).

Hypotheses that female humpback whales obtain information about singing males via songs, or that males assess the fitness of other males through song are 'only viable if songs exhibit reliably perceivable inter-individual differences' (Tyack, 1981). Studies of odontocetes confirmed the existence of individual-specific, stereotyped whistles, called signature whistles, and these have been implicated in direction communication between individual bottlenose dolphins (Caldwell et al., 1990; Tavolga, 1983).

The evolution of song over time would tend to work against the development of individual-specific information, at least in song pattern and structure. A more reliable identifier may be in acoustical characteristics of sound types. Research into the acoustical properties of humpback whale song has focused primarily on qualifying the characteristics of sound types, describing the overall pattern of the song and documenting song evolution across years (Payne et al., 1983; Guinee et al., 1983; Payne & Payne, 1985; Mednis, 1992). Inter-individual variability in the acoustical characteristics of sound types, although identified, has been not been extensively researched. Payne & Payne (1985) noted that inter- and intra-individual variability existed but variation between songs of consecutive years was much greater. Hafner et al. (1979) suggested that individual-specific information could be encoded within the 'cry' component of songs. However, comparisons of cries were obtained from only five whales over a three-year period. Frankel (1994) measured four parameters for each of six sound types and demonstrated significant differences between whales for each of the variables. He concluded that individual-specific information could be contained within sound types but did not investigate further.

If there is significant variability in the acoustical characteristics of the same sound type sung by different individuals, and this variability is consistent within individuals, individual-specific information may be encoded within the song. Further, such information might be used by females in selecting males for reproduction.

Here we qualitatively describe the structure and pattern of the song and conduct a detailed quantitative analysis of the acoustical characteristics of selected sound types to determine if these contain information that allows discrimination between individuals. An understanding of the characteristics of humpback whale song and how song varies between individuals will augment current knowledge pertaining to song function, the role of song in the reproductive process, and may provide a clearer understanding of the species' social structure.

METHODS

STUDY SITE. Point Lookout, North Stradbroke Island (27°26'S, 153°33'E) is situated ~18km off the southeast Queensland coast (Fig. 1). During winter humpback whales migrate along the coastline with most passing within 10km of the shore at Point Lookout (Paterson, 1991). Recordings of humpback whale song were obtained from 20th to 31st July 1998. This period was chosen to avoid the confusion from multiple singers evident closer to the peak of the northward migration which occurs late June to early August (Paterson et al., 1994; Bryden et al., 1990; Brown et al., 1995).

RECORDING EQUIPMENT. Recordings were obtained using a bottom-mounted buoy developed by the Defence Science and Technology Organisation, Sydney, with some modifications specified for this project. The hydrophone-buoy was a spar buoy design, constructed of pressure PVC piping supported by a fibreglass torus float and maintained in position by an anchor on the sea floor. The buoy was anchored ~3km offshore in 30m of water.

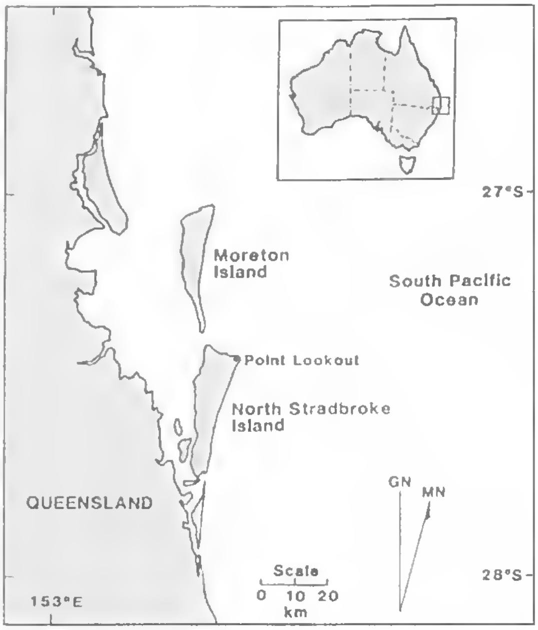

FIG. 1. Study site. Hydrophone-buoy was positioned ~3km offshore, east of Point Lookout.

The hydrophone was a GEC marconi SH101X connected to an RANRL pre-amplifier and housed in a separate PVC canister underwater to avoid electromagnetic interference and suspended at a depth of 17m. The pre-amplifier had a 40dB gain and 1MΩ input impedance. Frequency response of the system was 30Hz-14,000Hz.

The signal was transmitted using VHF and received by a vertically polarised YAGI antenna connected directly to a 4-channel VHF radio receiver (type 8101). Recordings were made directly to a Sony TCD-D7 Digital Audio Tape recorder (DAT). The received signals also ran directly into a desktop computer for real time analysis using Spectrogram 4.2.10 (developed by R.S. Horne).

DEFINING AN INDIVIDUAL. No information on sex or age of individuals was obtained and it was not possible to positively identify individual whales. Therefore, the following assumptions and guidelines apply. 1) Singers recorded on different days were different individuals. Recordings were obtained from the migration pathway therefore individuals were mobile and did not remain within acoustic range of the hydrophone for extended periods. Observations have shown that whales are clearly in transit as they pass Stradbroke Island (Paterson, 1984; Cato, 1984) and singers have been observed travelling at speeds greater than 1km per hour (Frankel, 1994; Helweg et al., 1992).

2) All recordings used in the analysis are unbroken, i.e. the recording of an 'individual' is continuous and there is no break or pause in singing (or recording).

3) As humpback whale song changes over time (Payne et al., 1983; Guinea et al., 1983, Cato, 1991) if any observed differences were to be associated with inter-individual variability, recordings must be considered contemporaneous, i.e. separated in time by no more than a few weeks (Cato, 1991). In this study the maximum separation time between recordings analysed is nine days. As changes in the song over such a short interval have been found to be negligible (Payne & Payne, 1985; Cato, 1991; Frankel, 1994; Helweg et al 1998), it is unlikely comparisons were confounded by temporal changes.

Each whale was given an identification number according to year/month/day/recording number, e.g. individual 807223 was recorded in 1998 on July 22 and was the 3rd recording made on that day.

ANALYSIS. *Spectrographic Analysis*. Sonagrams were created using the PC-based sound analysis software Spectrogram (v. 4.2.10). Initial inspection of sonagrams indicated that the majority of sound energy lay below 4kHz. Thus, recordings were digitised with 16-bit resolution at a sampling rate of 5.5kHz. Sonagrams were generated with a Fast Fourier Transform (FFT) of 1024 points yielding a 5.4Hz frequency resolution and 186msec time resolution.

Pattern Analysis. Descriptive names were used to identify particular sound types, e.g. 'growl', 'down moan', 'high cry', 'bellow'. Once each sound type had been assigned a label it was possible to identify the order and timing of the phrases, themes and subsequently the pattern of the song for each individual using a combination of aural and spectrographic analysis.

Statistical Analysis. We identified two sound types on which to base a quantitative statistical analysis of variability. These sounds were chosen as initial aural examination suggested that they were quite variable and because the spectrographic parameters could be measured with little ambiguity.

Sound type 1 was a narrow-band frequency modulated sound with associated harmonics. Initial analysis demonstrated that it was possible to obtain a reasonable approximation of the frequency contour by measuring the following variables: start frequency (Hz); end frequency (Hz); number of inflection points; frequency (Hz) and time (ms) at each inflection point; frequency range, expressed as the ratio of the maximum to minimum frequencies (Hz); duration (ms). The ratio of frequencies between the start and the first inflection point and at the first and second inflection points were also calculated. An inflection point is defined as a change in the slope of the frequency contour from positive to negative or vice-versa. Time and frequency were recorded at the point where the slope of the frequency contour moved through zero, or as close to this point as was possible.

Sound type 2 was a short, narrow-band sound with little frequency contouring. Each sound unit was divided into four equal sections and the following variables were measured: start frequency (Hz); frequency at 1/4 point (Hz); frequency at midpoint (Hz); frequency at 3/4 point (Hz); duration (msec); frequency range (Hz). We used ratios rather than absolute differences in frequencies because studies of hearing suggest that the perception of frequency can be related to a logarithmic scale of frequency, i.e. perception is of relative rather than of absolute frequency (Yost, 1994).

For both sound types, the sound units measured were selected from the same part of the song, being the first occurrence of the theme after a surfacing, as determined by the audible drop in level associated with surfacing behaviour (Cato, 1991). Generally, the units measured were the first occurrence of the sound type for each phrase, however, as some sound units could not be measured accurately, due to interference masking some portion of the sound, the sound unit from the phrase immediately following was measured. Both sound types analysed came from the same song.

Univariate and Multivariate Statistical Analysis. To investigate differences between individuals, based on all variables, a 1-way multivariate analysis of variance (MANOVA) was performed. Post hoc tests were examined to identify which individuals were significantly different according to each variable. Kruskall-Wallis ANOVA's were run for each variable to identify specific dependent variables that contributed to the significant overall effect.

Canonical Discriminant Function Analysis. To determine whether individuals could be discriminated statistically based on a set of given variables, a canonical discriminant function analysis (CDA) was run.

RESULTS

The survey period yielded 68 hours of recordings across a 12-day period. Continuous recordings, of a reasonable length (minimum of 9 complete song cycles) and good signal to noise ratio, were obtained for 7 individuals. A total of 25hr of recordings from 7 individuals was analysed to describe the song structure.

DESCRIPTION OF SOUND TYPES. Frequencies of all sound types (including harmonics) were in the range of 50Hz-6000Hz which is ~7 octaves. Nine distinct sound units were identified which were grouped into five themes. Sound types varied from acoustically simple to complex and were classified into four broad categories (Table 1). Each category is described by its frequency range, fundamental frequency and duration. The lowest in frequency were the 'growl' and 'bwop' sound units and the highest frequency units were the 'squeak' and 'high cry' (Table 1).

DESCRIPTION OF SONG PATTERN. *Phrase and Theme Structure.* The phrase structure, including order of occurrence and number of occurrences of each sound unit is presented in Table 2. Phrases contained either two or three sound types. These were grouped into 5 themes: A-E. Sub-themes were identified by the number of occurrences of the second sound type and/or the presence of a third sound type. All themes except theme E had sub-themes. However, only sub-theme Bs is included in the table as this was the only sub-theme which incorporated a 'new' sound. The order of the sound units within each phrase was fixed and occurred invariantly, however the grunts in theme A and D were not present in all phrases.

Theme A. Arbitrarily designated as the start of the song as it was usually the first theme sung after the attenuation (indicative of when the individual moved to the surface to breathe). Phrase length was determined by the number of sound units within the theme. Mean duration = 12.84sec (±2.70SD; n = 63) (Fig. 2).

Theme B. The start was signalled by a series of 2-3 'high cries', a truncated 'transitional phrase' (Payne & McVay, 1971), with a mean duration of 4.98sec (±0.51SD; n = 63). All subsequent phrases began with a single 'modulated bellow', followed by 1-3 'high cries' (Fig. 3). The interval between the 'high cries' and the 'modulated bellow' was longer (1.6sec) than the interval between the 'modulated bellow' and 'high cries' (1.0sec). Therefore, we identified the start of each phrase as beginning with the 'modulated

TABLE 1. Classification of sound units into sound type categories and description of temporal and spectral characteristics. * = frequency range includes harmonics obtained from good SNR recordings.

Sound Type	Frequency Range *(Hz)	Duration (sec)	Fundamental Freq. (Hz)
Harmonic			
Downmoan	120 - 4000	3.0 - 4.6	120 - 200
Modulated bellow	200 - 4000	0.9 - 1.5	190 - 520
High cry	450 - 6000	0.4 - 1.5	450 - 2000
Downsweep	100 - 4000	0.5 - 1.5	100 - 425
Broadband Continuous Sounds			
Growl	100 - 1700	0.8 - 1.2	
Broadband Pulsative			
Grunt	160 - 1700	0.08 - 0.16	166 - 210
Squeaks	780 - 4500		
Complex			
Bwop	60 - 2000	0.1 - 0.4	60 - 115
Uptrill - growltrill - trill	200 - 3000	2.6 - 3.0	 200 - 350 350 - 1000

TABLE 2. Phrase and theme structure. Sound units in order of occurrence and number of occurrences for each phrase and theme. * = minimum number of occurrences. As individuals usually surface during this theme it was not possible to record all occurrences due to attenuation of the sound. # = high cries present only at start of the theme. Each subsequent phrase began with the modulated bellow followed by high cries.

Theme	Sound Units in Order of Occurrence (phrase)	No. of Occurrences of Sound Unit (per phrase)	No. of Occurrences of Phrase (per theme)
A	Downmoan Growl Grunt	1 1-2 3-12	4-13 *
B	High cry # Modulated bellow High cry	2-3 1 2-3	8-14
Bs	Modulated bellow Squeaks	1 4-6	3-6
E	Downsweep Squeaks	2 4-8	1-5
C	Downsweep Bwop	1-2 1-3	9-32
D	Uptrill Growl Grunt	1 1-2 3-12	1-22

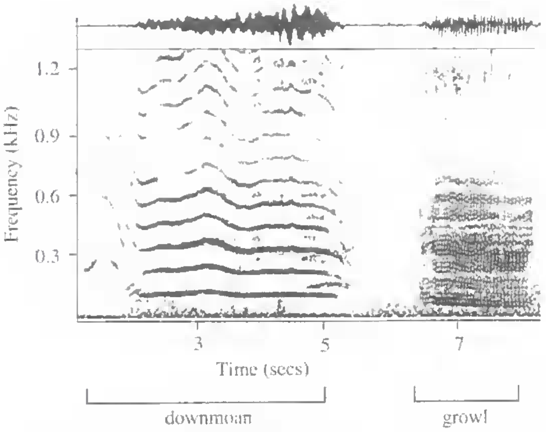

FIG. 2. Sonagram of phrase structure of theme A, comprising three sound types: 'downmoan', 'growl' and 'grunt train'. 'Grunt train' was not present in all repetitions and is omitted in this phrase. Sampling rate = 5.5kHz, FFT = 1024 pts.

bellow'. Three sub-themes were identified and defined by the number of occurrences of the 'high cry'. Sub-theme 4 (Bs) comprised the modulated bellow and a series of squeaks and was repeated between 3-6 times before the singer moved on to the next theme (Fig 3).

Theme E. Appears to be a transitional theme containing one sound type from the preceding theme (B) and one from the following theme (C). However, unlike a single transitional theme, the phrase is repeated 1-5 times which is the defining feature of a theme. Mean phrase duration was 7.76sec (SE ± 0.59; n = 63) (Fig. 4).

Theme C. An evolving theme with a systematic change in the duration and frequency range of both sound types (Fig. 5). The 'downsweep' showed some variation in acoustic character depending on the position of the sound unit within the theme. There was a gradual change in the frequency range, frequency contour and duration of the sound unit as the theme progressed. In the first phrase the 'downsweep' had a mean duration = 0.5sec (±0.47SD; n = 63) and the final occurrence had a mean duration = 1.5sec (±0.76SD; n = 63). 'Downsweeps' occurring early in the theme had an initial rise before falling with a frequency range of 120Hz-240Hz. As the theme progressed the frequency contour flattened and became a level moan with a frequency range between 100Hz-145Hz.

The 'bwop' also exhibited similar variation in acoustic characteristics depending on the position. Duration of 'bwops' at the beginning of the theme was approximately 0.24sec with a fundamental frequency contour of ~130Hz. As the theme progressed the sound type lengthened to 0.5sec and the fundamental frequency decreased to ~40Hz (Fig. 5). Three sub-themes were identified defined by the number of occurrences of the 'bwop' which varied between 1 and 3.

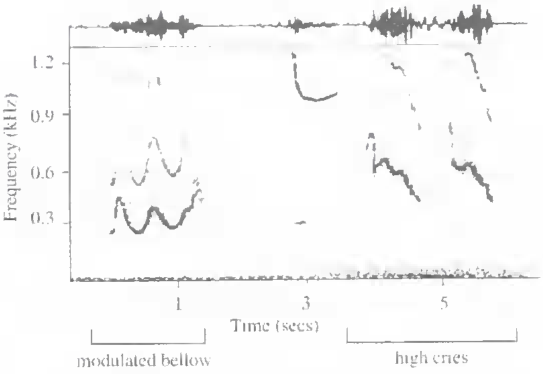

FIG. 3. Sonagram of phrase structure of theme B, comprising two sound types: 'modulated bellow' and 'high cries'. Number of 'high cries' varied from 1-3 throughout the theme. Sampling rate = 5.5kHz, FFT = 1024 pts.

Theme D. Each theme consisted of 1-22 phrases. Mean duration of the phrase was 11.4sec (±1.69SD; n = 63) (Fig. 6).

Song Structure. The five themes occurred in the order A-B-E-C-D. Average song length was 7.99min (±2.61SD; n = 115). Maximum song length was 12.93min and the minimum 5.13min. Average song bout (period of singing between surfacings) was 11.10min ± 2.48SD. Song bouts often contained more than one song cycle,

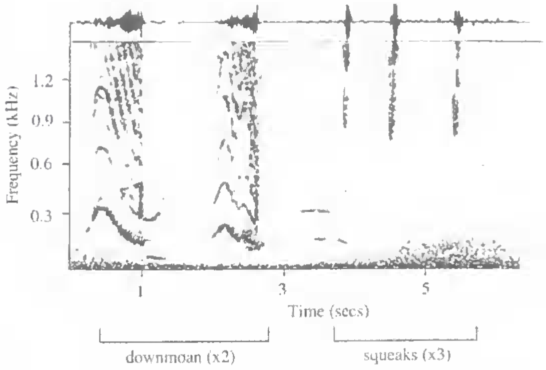

FIG. 4. Sonagram of phrase structure of theme E, a transition theme containing two sound types: 'downsweep' and 'squeaks'. Sampling rate = 5.5kHz, FFT = 1024 pts.

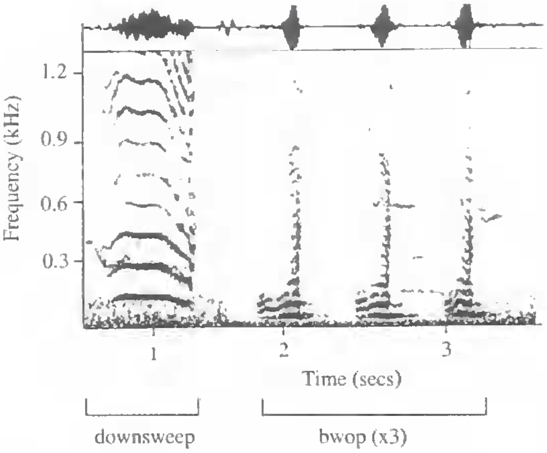

FIG. 5. Sonagram of phrase structure of theme C, comprising two sound types: 'downsweep' and 'bwop'. Number of 'bwops' increased progressively from 1 to 3 as the theme continued. Sampling rate = 5.5kHz, FFT = 1024 pts.

although never more than three. If greater than one song was sung during a song bout, theme A was often omitted and individuals would begin the second song with theme B. This was not a consistent feature either within or between individuals, however it suggests that theme A is a link between song bouts rather than a link between songs cycles. The first song of a song bout was longer (mean 7.366min ± 1.609SD) than the second song (mean 5.320min ± 1.576SD).

One aberrant song was identified. Individual 807201 omitted theme B from all songs. The mean song duration was 5.27min (±1.43SD; n=9).

MULTIVARIATE AND UNIVARIATE ANALYSIS. The two sound types used for the analysis of acoustical characteristics are the 'modulated bellow' from theme B and the 'downsweep' from theme C. Theme A could not be used as most individuals surfaced during this theme and the resulting attenuation prevented accurate measurements. Theme E was a transitional theme and contained sound types from the preceding and following themes, B and C respectively.

Sound Type 1 - Modulated bellow (Mb). Eight sound units were measured from each of 9 songs for each of the 6 individuals (n = 72). Individual 807201 was not included in the quantitative analysis as theme B did not occur in any of the songs recorded. A MANOVA on the $\log_{10}$ transformed data showed a highly significant difference between individuals (Wilks' Lambda = 0.242; df 45, n = 72; 1872; p <0.01). Non-paramctric univariate tests demonstrated a highly significant difference between individuals for each of the 9 variables (Table 3).

Box and whisker plots (±1.96SE) for each variable were created from the multivariate tests to identify variation between individuals. Only three plots have been reproduced here (Fig. 7A-C). There were significant differences between some individuals for one variable and very little variation between the same individual for another variable, with no individual consistently different from the rest.

Although there were significant differences between individuals the variation in the frequency of any frequency variable between individuals is small. For example, the variation in the frequency (1.96 × standard error) of the start point (Fig. 7C) for an individual is <0.07 on the logarithmic scale, i.e. about 4%, which corresponds to a difference of <1 semitone. Four individuals show only 1.1% difference in the mean of the start frequency (Fig. 7C). Total variation across all whales was <12% which corresponds to a change in frequency of 2 semitones. The greatest variation in frequency range between individuals is for the ratio of frequencies between inflexion points 1 and 2 at about 23%, less than 4 semitones (Fig. 7B).

Sound Type 2: Downsweep (Ds). Three sound units from 9 songs for each of the 6 individuals

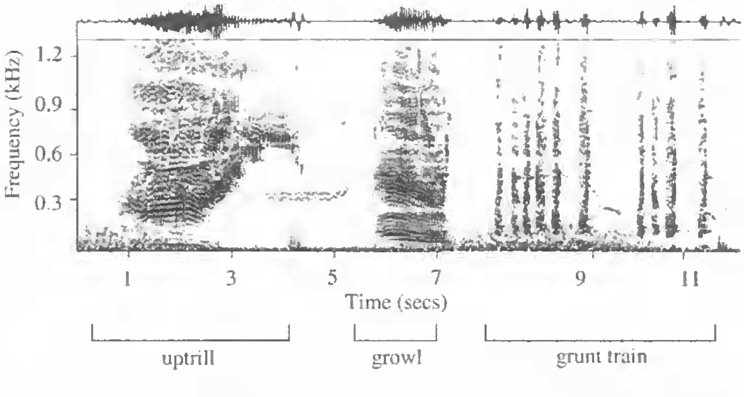

FIG. 6. Sonagram of phrase structure of theme D, comprising three sound types: 'uptrill', 'growl' and 'grunt train'. 'Grunt train' was not present in all repetitions. Sampling rate = 5.5kHz, FFT = 1024 pts.

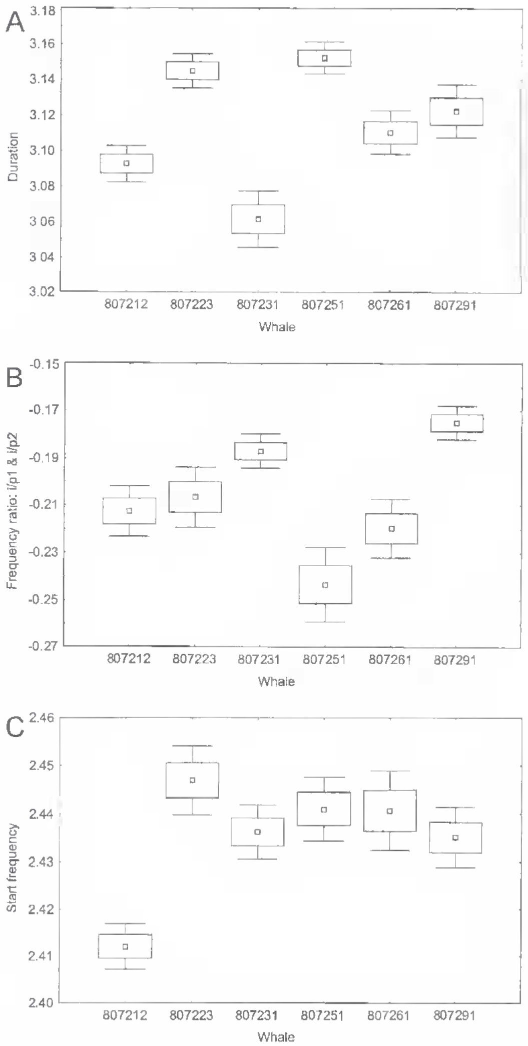

FIG. 7. Box & whisker plots for sound type 1 (modulated bellow) for each whale for the variables: A, 'duration'; B, 'frequency ratio between i/p1 and i/p2'; C, 'start frequency'. Mean, ±1SE (box) and ±1.96SE (bar). All values are $\log_{10}$ transformed.

were included in the analysis (n = 27). The MANOVA showed significant differences between individuals (Wilks' Lambda = 0.081; df (35,633); p <0.01). The Kruskall-Wallis ANOVA by Ranks run on each variable independently shows significant differences between individuals for all variables except end frequency (Table 4). Box & Whisker plots (±1.96 SE) derived from the MANOVA show the variation between individuals for three variables (Fig. 8A-C).

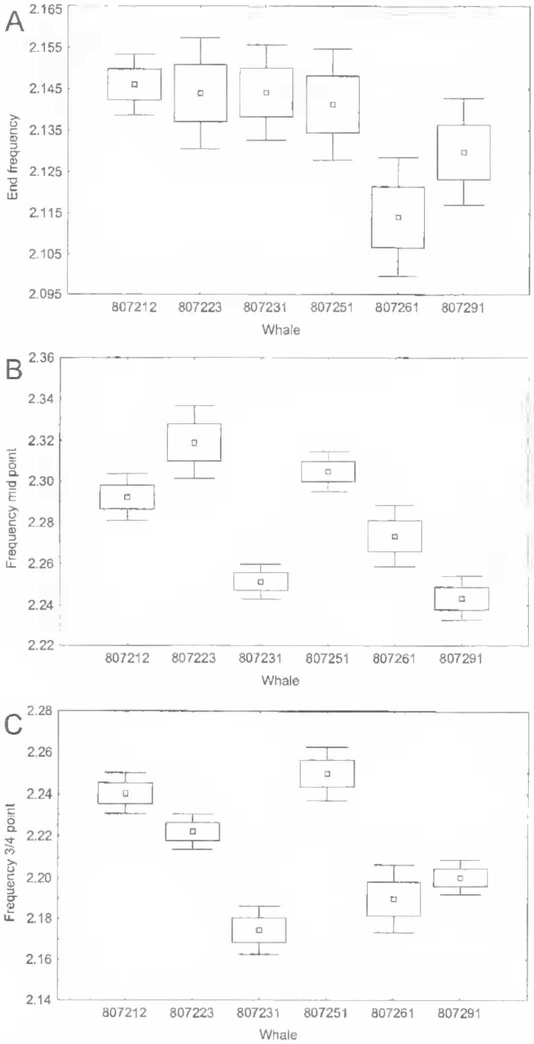

FIG. 8. Box & whisker plots for sound type 2 (downsweep) for each whale for the variables: A, 'end frequency'; B, 'frequency at midpoint'; C, 'frequency at ¾ point'. Mean, ±1SE (box) and ±1.96SE (bar). All values are $\log_{10}$ transformed.

Variation between individuals for each variable is similar for sound type 2 as was found for sound type 1. Although there are significant differences between individuals for each variable the difference between individuals with respect to frequency changes is very low. The greatest difference in frequency values between individuals was 4 semitones. End frequency showed a frequency range of only 2 semitones which corresponds to a 12% change (Fig. 8A).

TABLE 3. Results of Kruskall-Wallis ANOVA for each variable tested independently. df (5); $p < 0.01$. All variables were $\log_{10}$ transformed. Sound type = modulated bellow.

Variable	Chi-sqr	p-level
Start frequency	41.425	p<0.001
End frequency	50.613	p<0.001
Frequency range	67.423	p<0.001
Duration	63.048	p<0.001
No. of inflection pts	49.018	p<0.001
Freq ratio start - i/p1	42.588	p<0.001
Freq ratio i/p1 - i/p2	89.556	p<0.001
Time diff. start - i/p1	50.817	p<0.001
Time diff. i/p1 - i/p2	25.750	p<0.001

CANONICAL DISCRIMINANT FUNCTION ANALYSIS. *Sound Type 1: modulated bellow.* A discriminant function analysis for multiple groups was carried out on the same nine variables. All variables were retained in the model and there was a highly significant level of discrimination between individuals: Wilks' Lambda = 0.241; F(45,1872) = 15.585; $p < 0.01$.

The canonical discriminant analysis (CDA) extracted five canonical roots (variables) from the data (number of groups minus 1). Chi-squared tests with successive roots removed indicated that the first four canonical roots resulted in a significant discrimination between groups ($p < 0.01$). However, the first 2 canonical roots accounted for 82% of the discrimination in the data set and so the remaining roots will not be discussed further. The contribution of the original variables to the first 2 canonical roots are shown in Table 5, expressed as standardised β coefficients. The β coefficient measures the respective variables contribution to the discrimination.

The first canonical root (CAN1) was dominated by the variables, frequency ratio start to i/p1(-1.499) and start frequency (-1.430) both negatively loaded (Table 5). The variable, time difference between i/p1 and i/p2 contributed the least (0.050). The contribution to Root 2 is dominated by the variables frequency ratio between start and i/p1 and frequency ratio between i/p1 and i/p2, both positively weighted with values of 1.524 and 1.339 respectively (Table 5).

The factor structure matrix indicates the simple correlations between the variables and canonical roots. The first canonical root (CAN1) is dominated by duration (-0.582) and number of inflection points (-0.539) both are negatively weighted (Table 6). CAN2 is dominated by the variables time difference between start and i/p1 (-0.519) and frequency ratio between i/p1 and i/p2 (-0.502). The variable with the least amount of correlation is start frequency (0.043) (Table 6).

TABLE 4. Results of Kruskall-Wallace ANOVA for each variable. df (5); N=162; $p < 0.05$. Sound type = downsweep.

Variable	Chi-sqr	p-level
Start frequency	28.253	p<0.001
Freq ¼ point	23.370	p<0.001
Freq midpoint	64.070	p<0.001
Freq ¾ point	39.044	p<0.001
End frequency	11.760	p=0.038
Frequency range	23.249	p<0.001
Duration	74.296	p<0.001

A two dimensional plot of the canonical scores for the modulated bellow using the factor matrix (Fig. 9) shows one individuals position relative to another. There is a high degree of overlap which indicates poor discrimination between individuals and no discrete clustering of individuals which would be expected if signature information was present (Fig. 9).

Sound Type2: downsweep. The discriminant function analysis showed a significant difference between individuals for six of the seven variables (Wilks Lambda = 0.0813; F(35, 633) = 14.76948; $p < 0.001$). Variable frequency range was not significantly different between individuals ($p = 0.427$).

The canonical discriminant analysis (CDA) extracted five canonical roots (variables) with the first four resulting in significant discrimination between groups ($p < 0.01$).

TABLE 5. Standardised β coefficients and Eigenvalue cumulative proportion for the first two canonical roots. All variables $\log_{10}$ transformed. Sound type = modulated bellow.

Variable	Root 1	Root 2
Start frequency	-1.430	0.587
End frequency	0.065	0.220
Frequency range	-0.391	-0.593
Duration	-0.447	-0.186
No. of inflection pts	-0.251	0.039
Freq ratio start – i/p1	-1.499	1.524
Freq ratio i/p1 – i/p2	-0.945	1.339
Time diff start – i/p1	-0.123	0.516
Time diff i/p1 - i/p2	0.050	0.405
Eigenvalues Cumulative proportion	0.9305 0.5054	0.5763 0.8184

TABLE 6. Factor structure matrix showing (pooled within-groups correlations) or (correlation variables) for canonical roots 1 and 2. All variables $\log_{10}$ transformed. Sound type = modulated bellow.

Variable	CAN1	CAN2
Start frequency	-0.279	0.043
End frequency	-0.156	0.144
Frequency range	-0.238	-0.432
Duration	-0.582	-0.069
No. of inflection pts	-0.539	-0.335
Freq ratio start – i/p1	-0.193	-0.199
Freq ratio i/p1 – i/p2	0.183	0.502
Time diff start – i/p1	-0.018	0.519
Time diff i/p1 – i/p2	0.070	0.127

The cumulative Eigenvalue showed 84% discrimination within the first two canonical roots (Table 7). The standardised β coefficients show duration provided the greatest contribution (0.91) followed to a much lesser extent by frequency range (0.37) (Table 7). CAN2 is dominated by the variable frequency at ¾ point (0.83) with duration contributing little to the discrimination (-0.096) (Table 7).

The factor structure matrix identifies duration as providing the greatest loading to CAN1 (0.806) with a lesser weighting by the variable frequency at midpoint (0.401) (Table 8). CAN2 is primarily weighted by frequency at ¾ point and is positively loaded, (0.829) with a lesser positive loading by the variable frequency at midpoint (0.513) (Table 8).

Canonical scores for CAN1 and CAN2 using the factor matrix correlations for the downsweep are plotted in Fig. 10. There is a level of discrimination between individuals 807223 and 807291 according to CAN1 (x-axis) which is dominated by duration. However, if individual-specific information is present, each cluster would be discrete for each individual. There is considerable overlap between individuals 807212 and 807251 (Fig.10), however it is unlikely they are the same individual as the recordings were separated by a period of 4 days. Further, they are well separated in Fig. 9.

DISCUSSION

SONG PATTERN AND STRUCTURE.The song pattern of the east Australian population of humpback whales during the northward migration in 1998 conforms to the structural 'rules' first described for populations in the northern hemisphere (Payne & McVay, 1971; Payne, 1983) and is similar to those described for this population (Cato, 1991). The song is well structured and comprises nine sound types which combine to form five themes. These themes occur in a fixed order and are a powerful constraint on the pattern of the song. Frequency range of all sound types was 50Hz-6000Hz and is similar to the frequency ranges published for the east Australian population (Mednis, 1991). Mean song duration was 7.99 minutes ± 2.61SD (n = 115). This is less than that described by Cato (1991) for the 1982-1983 song (for the same population), which had a mean duration of 9.25min. Variation in song duration between years is most likely a result of the difference in the number of sound types and themes.

TABLE 7. Standardised β coefficients showing the contribution of each variable to the first two canonical roots. All variables $\log_{10}$ transformed. Sound type = downsweep.

Variable	CAN1	CAN2
Start frequency	0.264	-0.468
Freq at ¼ point	-0.125	0.228
Freq midpoint	0.247	0.524
Freq at ¾ point	0.029	0.834
End frequency	0.311	-0.542
Frequency range	0.372	-0.354
Duration	0.914	-0.096
Eigenvalue Cumulative proportion	2.349 0.569	1.133 0.844

DISCRIMINATION BETWEEN INDIVIDUAL SINGERS. Both multivariate and univariate tests showed significant measurable differences between individuals for all parameters included in the analysis. However, there was no observable pattern and no consistent differences between individuals. If differences in song pattern and structure are to be useful, differences would be

TABLE 8. Factor structure matrix for CAN1 and CAN2. All variables $\log_{10}$ transformed. Sound type = downsweep.

Variable	CAN1	CAN2
Start frequency	0.304	-0.162
Freq at ¼ point	0.295	0.084
Freq midpoint	0.401	0.513
Freq at ¾ point	0.069	0.829
End frequency	0.010	0.133
Frequency range	0.309	-0.009
Duration	0.806	-0.149

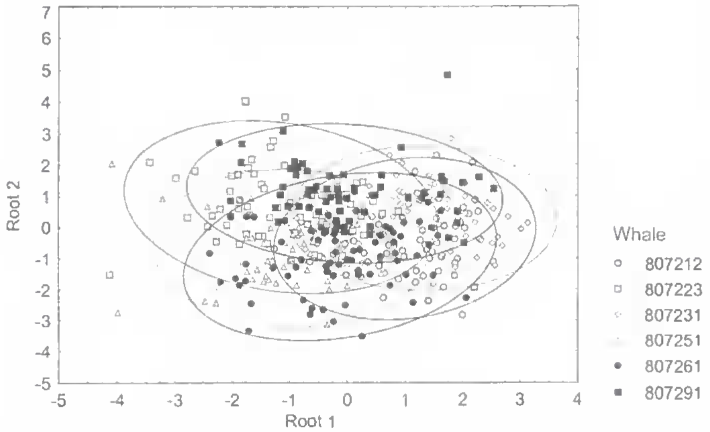

FIG. 9. Scatterplot of canonical scores for sound type 1 (modulated bellow). CAN 1 & CAN 2 accounted for 82% of discrimination. CAN 1 is dominated by the variables 'duration' and 'number of inflection points', both negatively weighted. CAN 2 is dominated by the variables 'time difference between start and i/p1' and 'frequency ratio between i/p1 and i/p2', both negatively weighted. Total variables in the model = 9.

expected to occur between all individuals for a particular variable.

The frequency range within each sound type shows that individuals consistently produce sounds which vary by <12% (2 semi-tones) and the variation in frequencies between individuals was ~23% (<4 semi-tones). The precision with which individuals produce each sound type suggests that humpback whales have a well-refined perception of frequency. Therefore, even small changes (~3 semi-tones) should be sufficient for an individual to be distinctive. Given the complexity of the song, the extensive time allocated to song production and the perceived importance of song in the reproductive cycle of humpback whales, producing consistent sounds may be important. The changes described in humpback whale song over time are cultural, in that they are due to learning of a vocal behavioural pattern (Payne & Payne, 1985; Cato, 1991). Noad et al. (2000) reported a rapid change in song over successive seasons and, terming it 'cultural revolution', suggested that novelty drives change. The apparent precision with which the humpback whales in this study produced sounds would facilitate this rapid change. However the rapid replacement of song would tend to work against development of individual differences.

Results of the canonical analysis demonstrated that most discrimination between individuals could be explained by duration, for both sound types analysed. Longer call duration has been demonstrated to be more attractive to female grey tree frogs (Gerhardt, 1991) and Pacific tree frogs (Whitney & Krebs, 1975). However, clusters are weak and there is considerable overlap between clusters suggesting poor discrimination between individuals. Increased signal duration has been related to increased energetic output in anurans and increased energetic cost of a signal appears to be a feature generally attractive to females in male display calls (Taigen & Wells, 1984). Helweg et al. (1992) suggested that song production in humpback whales may represent a relatively small portion of the energy budget and suggested it is unlikely that females use duration as a measure of energetic output.

Stereotypy of humpback whale song is one characteristic which has been stressed in the literature. Complexity, however, can be seen in the ways that singers vary the songs they produce

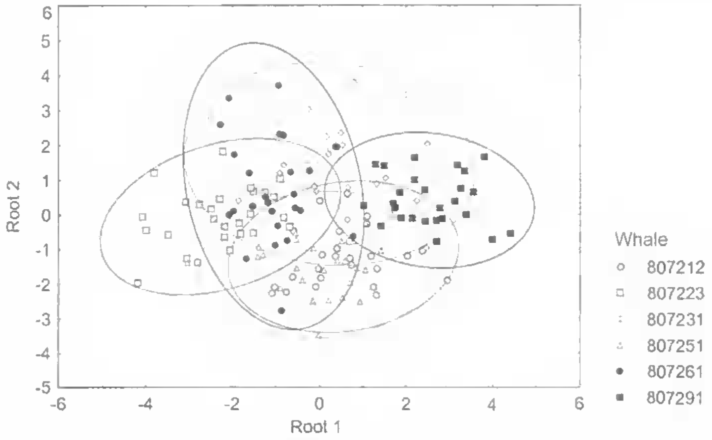

FIG. 10. Scatterplot of canonical scores for sound type 2 (downsweep). CAN 1 & CAN 2 accounted for 84% of discrimination. CAN 1 is dominated by the variables 'duration' and 'frequency at midpoint', both positively weighted. CAN 2 is dominated by the variables 'frequency at ¾ point' and 'frequency at midpoint', both positively weighted. Total variables in the model = 7.

within a single session, for example in terms of how many times each phrase is repeated. Within-population studies among European warblers and other species has revealed a relationship between repertoire size and components of fitness. European warblers with larger repertoire sizes may pair earlier (Catchpole, 1983) or obtain more mates (Catchpole, 1986). Yasukawa et al. (1980) found a correlation between repertoire size and harem size in red-winged blackbirds.

If repertoire size could be paralleled with song complexity in humpback whales then perhaps the functional unit of humpback whale song is the pattern and degree of complexity within phrases and themes rather than the acoustical characteristics of the component parts. Tyack (1981) argued that song complexity is the result of inter-sexual selection. This implies that active female choice has occurred. Theories of sexual selection based on female choice rely upon the assumption that females actively choose their mates, rather than just experiencing passive attraction to the nearest male stimulus. Active choice must involve sampling several males and rejecting some before a choice is made. Dale et al. (1990, 1992) demonstrated that female pied flycatchers visit up to nine singing males before selecting a mate. Female great reed warblers take up to three days to select a mate and during this time will visit, on average, six male territories before making a selection (Bensch & Hasselquist, 1992).

For humpback whales, Helweg et al. (1992) proposed that singers maintain a 'spatially dynamic array through which females pass'. Females can then listen to singers and select a mate based on some characteristic within the song. Tyack (1981) found that singers frequently joined, or were joined by, other whales which resulted in the cessation of singing. Further, some of the whales which joined singers were determined to be females lending support to the theory that singing serves to attracts females (Tyack, 1981; Medrano, et al., 1994).

However, females may not actively choose males; 'selection' may closer reflect passive choice, whereby females exercise choice by allowing potential mates to join her (Helweg et al., 1992; Frankel, 1994). Results from playback experiments have shown that few whales approach the playback of song (Tyack, 1983; Mobley et al., 1988). The most 'attractive' vocalisations are feeding calls or social sounds, which are indicative of a female being present. During both summer and winter the social structure of humpback whales is fluid with many small groups associated for brief periods. However, larger groups are often seen during the winter migration. In these larger groups substantial surface activity occurs, ranging from low level 'passive' behaviours to direct physical contact between members. These 'competitive' groups consist of multiple mature males competing for sexual access to a single mature female (Tyack & Whitehead, 1983; Baker & Herman, 1984; Clapham, et al., 1992). Females then select mates based on outcomes of these competitive associations. Therefore, song may function to advertise location to both males and females, but it may be the results of direct competitive behaviour between males that influences female choice.

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